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Are correlations between deadwood fungal community structure, wood physico-chemical properties and lignin-modifying enzymes stable across different geographical regions?

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ABSTRACT

Wood-inhabiting fungi are major agents of wood decomposition. However, it is unclear which factors determine their distribution and enzyme production. Many studies that have addressed this issue suffer from a lack of geographic extent. Here, we investigate the fungal community structure of 117 *Fagus sylvatica* logs in relation to wood physico-chemical properties and secreted ligninolytic enzymes, across three distinct geographical regions of Germany. Our results revealed that fungal community structure was similar across different regions, but was nevertheless variable in all regions. The relationships between fungal community structure, wood physico-chemical properties and enzyme activities were not consistent across different regions. However, we identified that the wood physico-chemical properties (i.e. decay class, remaining mass, density, extractives, total lignin and pH) were the most important factors associated with the fungal community structure in all three regions. In contrast, the wood physico-chemical properties and the fungal community structure did not sufficiently explain variation in the detected enzymatic activities. Thus, we assume that interspecific interactions and recently described priority effects play more important roles in the production of lignin modifying enzymes.

1. Introduction

Decomposition of wood is essential in carbon dynamics and nutrient cycling in forest ecosystems (Cornelissen et al., 2012; Kahl et al., 2012; Rajala et al., 2012; van der Wal et al., 2013, 2014; Peršoh, 2015). It is a complex ecological process, which is regulated by different drivers: climate, substrate quality (tree species) and the abundance, composition and activity of the decomposer communities (Weedon et al., 2009; Herrmann and Bauhus, 2013; Liu et al., 2013). A recent work has demonstrated that climate alone failed to predict wood decomposition rates at regional scales, while local-scale factors were found to be much more important for explaining most of the variation (Bradford et al., 2014). Other studies indicate that substratum (e.g. litter) quality may be more important than climate in controlling decomposition rates across different biomes (Cornwell et al., 2008; Weedon et al., 2009; Bradford et al., 2014).

Due to its high amount of lignin, deadwood is difficult to decay (Floudas et al., 2012). Under natural conditions, only fungi substantially decompose deadwood. With their ability to use a battery of secreted oxidoreductases and hydrolases (wood decomposition enzymes), they are considered as the primary wood decomposers and among them are the only organisms which are able to decompose lignin (Cornelissen et al., 2012; Stokland et al., 2012; Purahong et al., 2014a, 2014b; Kubartová et al., 2015; Peršoh, 2015). Diverse bacteria also colonize deadwood and form at least commensal interactions with wood-inhabiting fungi, for example, by providing additional nitrogen (de Boer et al., 2005; Hoppe et al., 2014, 2015a). However, due to their limited ability to decompose polymeric lignocelluloses, bacteria are thought to play only a minor role in wood decomposition (Cornelissen et al., 2012). Distribution

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patterns of wood-inhabiting fungi provide distinct information to predict their roles in ecosystem functions and stability (Kubartová et al., 2012). The fungal community structure can be influenced by various biotic and abiotic drivers. As one biotic driver, priority effects might play an important role for fungal community assembly (Boddy, 2000; Fukami et al., 2010; Dickie et al., 2012; Hiscox et al., 2015). The first arriving fungus significantly changes the assembly of the entire fungal community that follows, and thus affects wood decomposition rates. On the other hand, it is still unclear how abiotic factors regulate the wood-inhabiting fungal community structure. Based on a limited number of studies, wood physico-chemical factors such as decay stage, log diameter, volume, density, C:N ratio, lignin content, macronutrients and a few micronutrients significantly correlate with the structure of wood-inhabiting fungal communities (Rajala et al., 2010, 2011, 2012). As decay progresses, these wood physico-chemical parameters change, which in turn corresponds to changes in the wood-inhabiting fungal community structure (Rajala et al., 2012). However, most studies that have addressed this issue suffer from a lack of geographic extent. It has recently been shown that, for example, latitude and mean annual temperature of distinct regions correlate with wood decomposition types (Fukasawa, 2015), and might therefore also impact the decomposer community. Both, climatic and management associated factors have also been shown to impact diversity patterns of sporocarps across beech forests in Europe (Ódor et al., 2006). Furthermore, the relation of wood-inhabiting fungal community structure and corresponding ecological function such as lignin decomposition is still rarely studied.

In this study, we investigated the correlation between fungal community structure, wood physico-chemical properties and ligninolytic enzyme activities in natural deadwood of *Fagus sylvatica* in temperate forests across different geographical regions of Germany (north to south gradient of approximately 600 km). Diverse wood physico-chemical properties, which were already reported to correlate with wood-inhabiting fungal community structure in previous publications are included in this present study (Rajala et al., 2010, 2011, 2012). Activities of three lignin-modifying enzymes: laccase (EC 1.10.3.2), manganese peroxidase (MnP, EC 1.11.1.13) and manganese independent peroxidases (MiP, EC 1.11.1.7/14/16 representing distinct protein families e.g. Kellner et al., 2014) were used as a proxy for fungal-mediated ecosystem functions. We hypothesize that different geographical regions of Germany harbour distinct fungal communities, which in turn results in consistent ecosystem functionality and thus consistent correlations with environmental factors.

2. Materials and methods

2.1. Sampling design

The study was conducted within the experimental research platform of the 'biodiversity-exploratories' in Germany (Fischer et al. 2010). Thirty forest plots (100 × 100 m) at three locations in different geographical regions were selected: the UNESCO Biosphere Area Schwäbische Alb (ALB) in south-western Germany (460–860 m a.s.l.), the National Park Hainich and its surrounding areas (Hainich-Dün) (HAI) in central Germany (285–550 m a.s.l.), and the UNESCO Biosphere Reserve Schorfheide-Chorin (SCH) in north-eastern Germany (3–140 m a.s.l.). The annual mean temperatures are in the range of 8–8.5 °C (SCH), 6.5–8 °C (HAI) and 6–7 °C (ALB) and the annual mean precipitation varies between 500 and 600 mm (SCH), 500 and 800 mm (HAI) and 700 and 1000 mm (ALB). The distances between different forest plots ranged from 0.315 km (within one experimental site) to 626.9 km (longest distance between plots in north-eastern and south-western Germany) (Fig. 1).

In May 2009, 117 naturally occurring downed deadwood logs of *F. sylvatica* were randomly selected in 30 forest plots in all three exploratories (Table S1). Three to seven wood samples were taken from each log (to better represent the entire log dimension) using a cordless Makita BDF451 drill (Makita, Anja, Japan) equipped with a 2 × 42 cm wood auger as described in Hoppe et al. (2014, 2015) and Purahong et al. (2014a, b). Data pertaining to the experimental forest plots and wood sampling are summarized in the supplementary data section and are explained in detail in Hoppe et al., 2014, 2015a and Purahong et al., 2014a, 2014b.

2.2. DNA isolation, PCR and ARISA (automated ribosomal intergenic spacer analysis) fingerprints

The total community DNA from 1 g wood powder of each sample was isolated using a modified CTAB-protocol (Doyle and Doyle, 1987). 900 μl of CTAB was added to the sample and the nucleic acid was separated from proteins and cell debris by adding 500 μl of 24:1 chloroform: isoamyl alcohol (Carl Roth, Karlsruhe, Germany) followed by another chloroform step (Carl Roth, Karlsruhe, Germany). DNA was precipitated by washing twice with ethanol (Merck, Darmstadt, Germany). Dried pellets were eluted in 100 μl molecular water (AppliChem, Darmstadt, Germany).

F-ARISA PCR (Ranjard et al., 2001) of each DNA extract was done in two replicates using a carboxyfluorescein FAM-labelled primer ITS1-F (5′-CTTGGTCATTTAGAGGAAGTAA-3′, Gardes and Bruns, 1993) and unlabelled ITS4 (5′-TCCTCCGCTTATTGATATGC-3′, White et al., 1990) in 30 μl reaction mixtures containing 6 μl FIREPol 5x Master Mix (Solis BioDyne, Tartu, Estonia), 15 μM of each primer and 1 μl template DNA. PCR was performed with an initial denaturation step at 95 °C for 5 min followed by 35 cycles at 95 °C for 60 s, 55 °C for 60 s and 72 °C for 75 s. Elongation was completed with a final step of 72 °C for 7 min.

PCR products were purified using the E.Z.N.A.® Cycle-Pure Kit (Omega Bio-Tek, Inc., Norcross, GA, USA). 10 ng of each purified PCR product was dissolved in 14 μl of deionized Hi-Di formamide (Applied Biosystems, Foster City, CA) with 0.1 μl of internal size standard Map Marker 1000 ROX (BioVentures, Inc., Murfreesboro, TN, USA). After denaturation for 5 min at 95 °C samples were chilled on ice for at least 10 min. Length heterogeneity of fungal ITS fragments was detected by capillary electrophoresis (ABI 3730xl, Applied Biosystems). Electrophoretic conditions were as follows: 7 s injection at 1.6 kV and separation at 15 kV for 3800 s. Row profiles were analysed using Gene Mapper software 4.0 (Applied Biosystems). All peaks above a threshold of 100 fluorescence units, which were presented in both technical replicates, were considered for further analyses (Purahong et al., 2015a, Moll et al., 2015). OTU binning was performed with the interactive and automatic R binning script (Ramette, 2009) using R (The R Foundation for Statistical Computing [http://cran.r-project.org/]). According to the script and its correlation values a window size of two was chosen.

2.3. Wood physico-chemical properties and enzyme assays

The concentration of C and N in wood samples was determined by total combustion using a Truspec elemental analyzer (Leco, St. Joseph, MI, USA). Klason lignin content was determined gravimetrically as the dry mass of solids remaining after sequential hydrolysis with 72% (v/v) sulphuric acid at 30 °C for 1 h followed with 2.4% H_2SO_4 (v/v) at 120 °C for 1 h (Effland, 1977; Liers et al., 2011). In a second step, acid soluble lignin was measured by UV-photometry according to Dence (1992) in the obtained hydrolysate. Total lignin was obtained by summing acid insoluble Klason lignin and acid

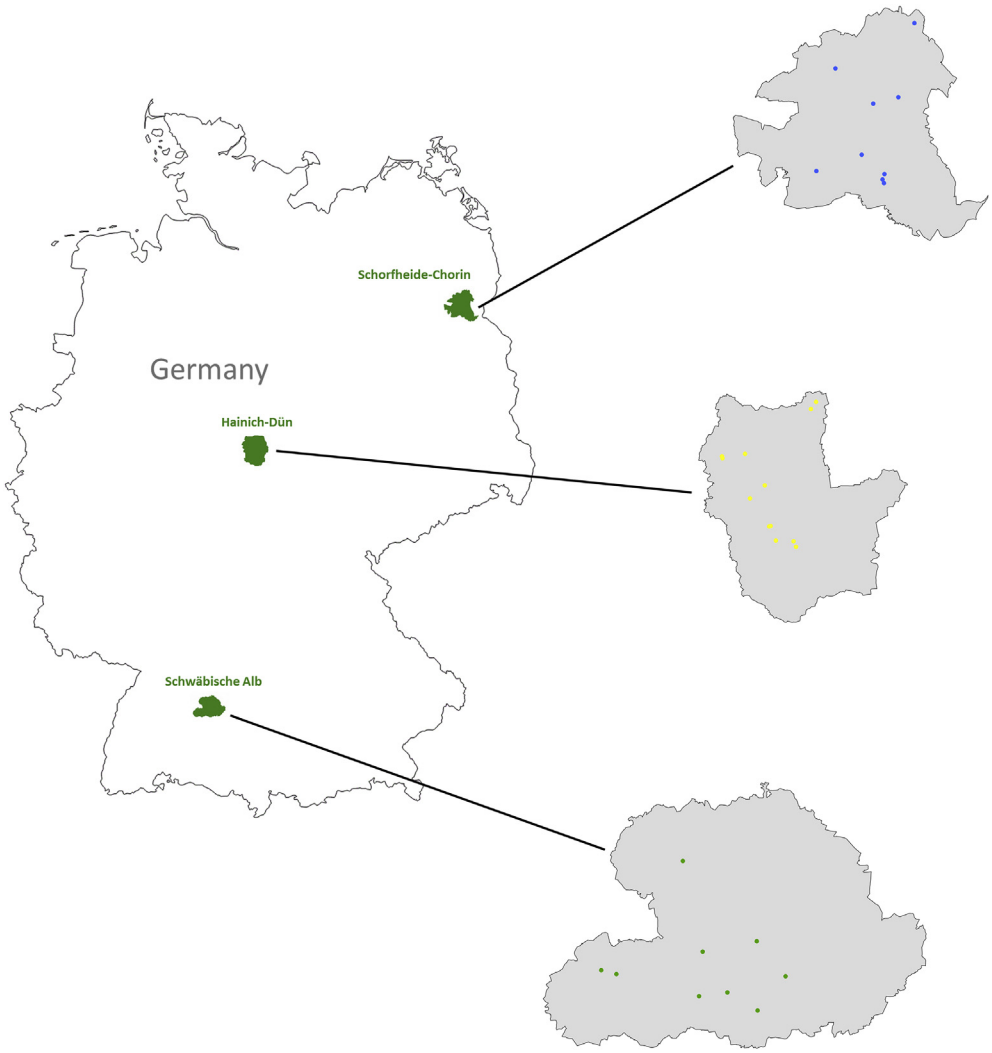

Fig. 1. Overview of the three experimental sites and their location within Germany. From north to south: UNESCO Biosphere Reserve "Schrofheide-Chorin", National park "Hainich" and UNESCO Biosphere Reserve "Schwäbische Alb".

soluble lignin (Raiskila et al., 2007). The wood samples' pH values and contents of nutrient ions and lignin-modifying enzymes were measured in aqueous extracts. The extractions were performed using 10 ml distilled water per 1 g dry mass of wood for 120 min on a rotary shaker (120 rpm). Macronutrients (Mg, K, Ca, Fe) and micronutrients (Cu, Mn, Zn, Ni) were determined using inductively coupled plasma (ICP) optical emission spectrometry (ICP-OES) and mass spectrometry (ICP-MS), according to the instrument manufacturers' specifications. Three oxidative extracellular oxidoreductases important for lignin decomposition (laccase – Lac, manganese peroxidase – MnP, manganese-independent peroxidases – MiP) (Hatakka and Hammel, 2011) were recorded. Activities of Lac and peroxidases were photometrically measured in the aqueous extracts in 96-well plates (F-bottom, Greiner Bio-One GmbH, Frickenhausen, Germany) with a plate reader (InfiniteM200, Tecan, Männedorf, Switzerland) by following the oxidation of ABTS (2,2′-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid), $\varepsilon 420 = 36.0\ cm^{-1}\ mM^{-1}$) according to Arnstadt et al. (2015). At first Lac activity was measured followed by peroxidase activity after addition of H_2O_2. Manganese-independent peroxidase (MiP) activity was detected in the absence of available Mn^{2+}-ions by using the chelator EDTA (5 mM, ethylenediaminetetraacetic acid). Thereby MiP activity represents a sum activity of a genetically diverse set of fungal peroxidases like lignin peroxidases, versatile peroxidases, generic peroxidases, dye-decolorizing peroxidases and unspecific peroxygenases (Hofrichter et al., 2010; Kellner et al., 2014). The MnP activity was measured in the presence of Mn^{2+}. The activities of MiP and MnP in each samples are considered independent (Purahong et al., 2014c). Nutrient ion and lignin-modifying enzyme analyses were conducted in triplicate and in duplicate, respectively, on the same subsamples.

Deadwood logs were assigned to four decay classes based on remaining mass (%) data by k-means cluster analysis as described in Kahl et al. (2012) and Hoppe et al. (2014) (Table S1).

2.4. Statistical analysis

All multivariate statistics were conducted on proportional abundance data using the relative fluorescence intensities of each sample. Analysis of similarities (ANOSIM) and nonmetric multidimensional scaling (NMDS) based on Bray-Curtis distances were conducted to investigate the fungal community structures using PAST (Hammer et al., 2001) and the 'vegan' package in R (Oksanen et al., 2013). Visualisation of 3D-NMDS was performed using the scatterplot 3D and rgl packages of R (Ligges and Mächler, 2003).

The correlations between selected wood physico-chemical properties and fungal community structure were investigated by fitting data on each factor to the NMDS ordinations of the fungal communities. The wood physico-chemical parameters considered in these analyses were decay class, concentrations of macronutrients (C, N, K, Ca, Mg, Fe) and micronutrients (Al, Cu, Mn, Ni, and Zn), relative wood moisture, wood density, remaining mass, total lignin and organic extractives, volume of each deadwood item and pH. Goodness-of-fit statistics (R^2) for environmental variables fitted to the NMDS ordinations of fungal communities were calculated using the *envfit* function of 'vegan', with *P* values based on 999 permutations (Oksanen et al., 2013). We calculated Spearman Rank correlations (pairwise comparisons) to link the wood physico-chemical properties to lignin-modifying enzyme activities for each geographical region using PAST (Table 1).

To investigate the impact of geographical distance on the fungal community structure, we performed Mantel Tests using Bray-Curtis dissimilarity matrices based on fungal OTUs and geographical distance matrices, which were calculated for all deadwood logs, using their spatial information on longitude and latitude.

3. Results

3.1. Geographical distribution of fungal OTUs

A total of 238 fungal OTUs were detected from all 117 deadwood logs in all three regions. The number of fungal OTUs detected in ALB was higher (227) than in HAI (198) and SCH (192) (Fig. 2). The mean number of fungal OTUs per deadwood log indicated significantly higher OTU richness in ALB (50.15) and SCH (52.07) than in HAI (35.82) ($F = 9.5$, $P = 0.0001$). Interestingly, the percentage of OTUs that were shared among all regions was very high (73.1%, 174 OTUs), whereas the percentages of OTUs specific at one (1.3–10.1%, 3–24 OTUs) or two (0.8–6.7%, 2–16 OTUs) regions were low. This was confirmed by one-way ANOSIM pair-wise comparisons of fungal community structures between all regions (Table S2). We did not observe significant correlations by comparing OTU-based community dissimilarities with the geographical distance of the observed deadwood logs (Fig. 3). These non-significant correlations were also consistent when exclusively comparing logs of the same decay class (Fig. S1). Accordingly, the results from one-way ANOSIM pair-wise comparisons of fungal community structures in deadwood at different regions revealed significant variations for different decay classes (Fig. 4).

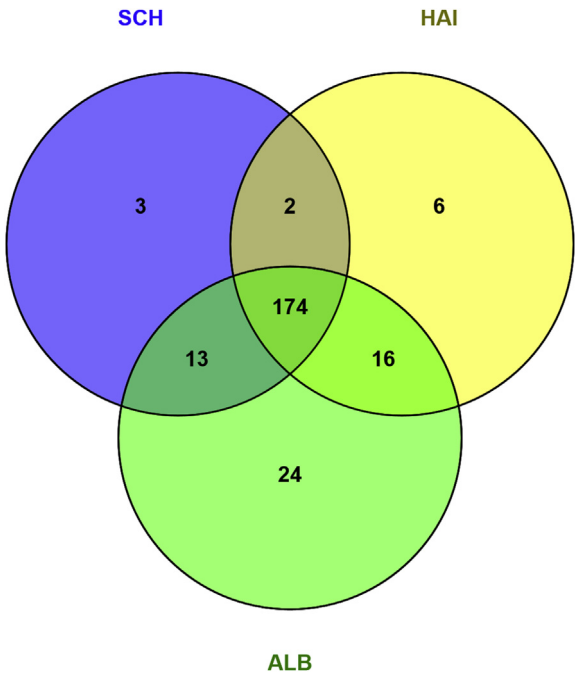

Fig. 2. Venn Diagramm displaying the unique and shared fungal OTUs across all three exploratories (ALB = Schwäbische Alb, HAI = Hainich, SCH = Schorfheide-Chorin).

3.2. Correlations between fungal community structure, wood-physico-chemical properties and ligninolytic enzyme activities

Decay class, remaining mass, density, extractives, total lignin and pH significantly correlated with fungal community structure in all three studied regions (Fig. 4, Table 2; potential autocorrelations are displayed in Table S3). N and Zn, taken as respectively representing a macro- and a micronutrient, significantly correlated with fungal community structure in two regions, while only a marginally significant correlation was found for N in the third region. Other elements (C, Ca, K, Al, Cu) correlated significantly with the fungal

Table 1
Relationships between mean activities of ligninolytic enzymes and selected wood physico-chemical properties revealed by Spearman rank correlation analysis. Significant correlations ($P < 0.05$) are displayed in bold. Marginal significant correlations ($P < 0.1$) are displayed in *italics*.

Wood physico-chemical properties	ALB			HAI			SCH		
	Lac	MiP	MnP	Lac	MiP	MnP	Lac	MiP	MnP
Decay class	0.12	**-0.52**	-0.02	-0.02	**0.40**	-0.22	0.26	-0.09	-0.14
Remaining mass	-0.13	**0.57**	0.01	0.01	**-0.45**	0.18	-0.26	0.02	0.08
Water content	0.18	**-0.49**	-0.04	0.21	**0.42**	-0.14	0.23	0.17	-0.07
Volume	-0.04	**-0.33**	0.28	-0.13	0.15	0.12	**-0.39**	-0.11	-0.11
Density	-0.11	**0.55**	-0.01	-0.02	**-0.43**	0.21	-0.31	0.01	0.04
C	-0.15	**0.49**	-0.03	0.04	-0.14	-0.13	-0.10	**0.41**	-0.32
N	0.01	-0.29	0.01	0.16	**0.34**	-0.13	0.30	0.01	-0.10
Total lignin	-0.16	**-0.46**	0.00	0.01	0.10	**-0.31**	0.23	-0.07	-0.09
pH	-0.15	**0.39**	0.10	0.05	0.07	-0.13	0.10	*0.37*	0.00
OTU richness	**0.35**	-0.26	**0.32**	-0.08	-0.02	-0.19	0.04	-0.03	0.11

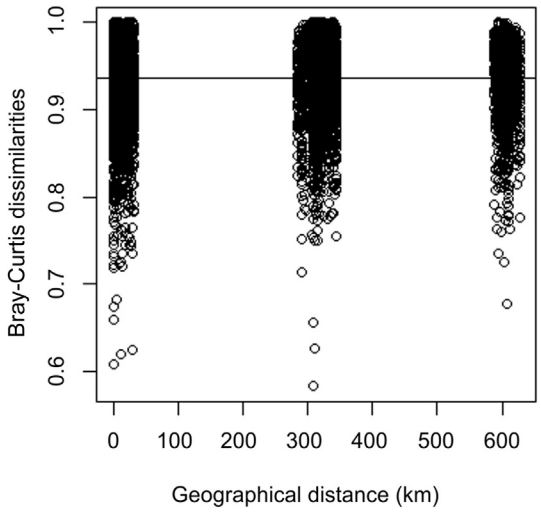

Fig. 3. Mantel Correlations between Bray-Curtis dissimilarities (based on OTU matrix) and geographical distance for all 117 deadwood logs.

OTU richness at ALB (Table 1).

4. Discussion

Our work combined fungal molecular fingerprints (F-ARISA), biochemical analyses and enzyme assays to investigate the relationships between fungal community structure, wood physico-chemical properties, and ligninolytic enzyme activities across different geographical regions in Germany. Surprisingly, we did not observe an impact of geographical distance on the fungal community structure, albeit having a unique shared pool of ~200 fungal OTUs, which contradicts our initial assumptions. Instead, even logs in close proximity displayed great dissimilarities, which might reflect that: i) fungal communities are present across a wide geographical distance, but priority effects and biotic and abiotic factors determine the community of each log (Fukasawa, 2015; Hiscox et al., 2015); and ii) successional variations occur in the course of wood decay (displayed by the different decay stages, Hoppe et al., 2015b). Despite the similarity of the fungal community structure in all regions, our results indicate that the communities

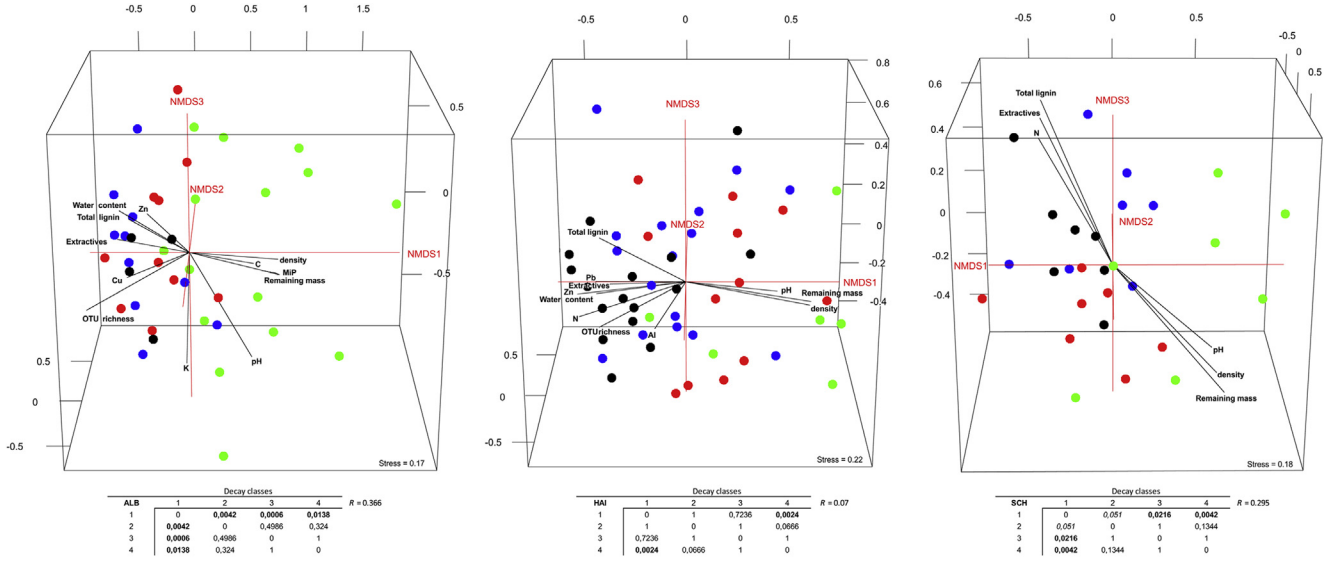

Fig. 4. 3D-Nonmetric multidimensional scaling (NMDS) ordinations of fungal community structure in all three exploratories (ALB = Schwäbische Alb, left cube; HAI = Hainich, middle cube; SCH = Schorfheide-Chorin right cube) using the *plot3d*, *scatterplot3D* and *ordigl* functions in R. The NMDS ordinations (stress = 0.17–0.22) were fitted to wood physico-chemical and anthropogenic factors by using the *envfit* command in 'vegan'. Different colours indicate different decay classes (green = decay class 1, red = decay class 2, blue = decay class 3, black = decay class 4). ANOSIM revealed significant separation of fungal community structure according to different decay classes, as displayed in the tables below the NMDS ordinations.

community structure only in one region (Fig. 4, Table 2).

Contrary to wood physico-chemical properties, none of the lignin-modifying enzyme activities correlated with fungal community structure in all three regions (Table 2). Only MiP activity was significantly correlated with fungal community structure at ALB ($F = 2.12$, $P < 0.01$). The result was confirmed by multivariate analysis of variance (distance-based redundancy analysis; dbRDA) based on the Bray–Curtis distance ($P < 0.01$) (Table S4). Correlations between lignin-modifying enzyme activities with a selection of wood physico-chemical properties varied strongly in different regions (Table 1). MiP at ALB positively correlated with remaining mass, C and pH but negatively with water content, whereas at HAI, MiP positively correlated with water content and N but negatively with the remaining mass. MiP at SCH positively correlated with C and pH. Laccase and MnP correlated only weakly positively with are not homogeneous and stable within a region. In addition, we found no relationship between fungal community structure and lignin-modifying enzyme activities. Even within one log there is a huge variation in enzyme activities, and they can vary across different parts of the mycelium of one fungus during the occupation of wood (Větrovský et al., 2010; Hahn et al., 2013). The set of secreted enzymes is specific to each fungus and displays different temporal patterns of secretion (Tuor et al., 1995; Liers et al., 2011; Hahn et al., 2013). True ligninolytic peroxidases including Mn-oxidizing enzymes as key enzymes (MnP) are only secreted by white-rot fungi (Hofrichter, 2002; Hatakka and Hammel, 2011). In consequence, not only the identity of the fungus is important but also its development in the community, which is the result of the priority effect and other interspecific interactions (Fukami et al., 2010; Arnstadt et al., 2015; Hoppe et al., 2015b). Wood-inhabiting

Table 2
Goodness-of-fit statistics (R^2) for parameters fitted to the nonmetric multidimensional scaling (NMDS) ordination of fungal community structure. The significance estimates were based on 999 permutations. Significant factors (Bonferroni corrected $P < 0.05$) are indicated in bold. Marginally significant variables (Bonferroni corrected $P < 0.10$) are indicated in italics.

Factor	ALB		HAI		SCH	
	R^2	P	R^2	P	R^2	P
Decay Class	0.5449	**0.001**	0.4459	**0.001**	0.5341	**0.004**
Remaining mass	0.5821	**0.001**	0.4168	**0.001**	0.5634	**0.002**
Water content	0.3336	**0.004**	0.2218	**0.012**	0.1983	0.143
Volume	0.1058	0.259	0.0282	0.724	0.0693	0.654
Density	0.5837	**0.001**	0.4098	**0.001**	0.4678	**0.008**
C	0.2027	**0.039**	0.0409	0.602	0.129	0.351
N	0.1841	*0.061*	0.3286	**0.002**	0.3822	**0.007**
Extractives	0.2983	**0.003**	0.163	**0.042**	0.4223	**0.005**
Total lignin	0.263	**0.009**	0.1885	**0.022**	0.5063	**0.001**
Laccase	0.0977	0.31	0.039	0.602	0.044	0.762
MiP	0.3067	**0.004**	0.0905	0.206	0.1417	0.343
MnP	0.0292	0.805	0.1118	0.142	0.1473	0.328
Mn	0.0521	0.623	0.1274	*0.094*	0.0462	0.775
pH	0.3742	**0.001**	0.3052	**0.002**	0.3818	**0.003**
Mg	0.106	0.271	0.1311	0.088	0.0754	0.583
Ca	0.2129	**0.039**	0.1367	*0.075*	0.094	0.49
K	0.2473	**0.023**	0.1581	*0.051*	0.1599	0.25
Fe	0.1201	0.251	0.0429	0.582	0.173	0.2
Al	0.1617	0.104	0.1864	**0.026**	0.1885	0.145
Cu	0.2352	**0.024**	0.074	0.31	0.1196	0.392
Zn	0.2153	**0.035**	0.3166	**0.002**	0.1816	0.179
Ni	0.1054	0.31	0.0173	0.858	0.0243	0.906
OTU richness	0.5276	**0.001**	0.338	**0.002**	0.2079	0.134

fungi are known to use biochemical defence mechanisms against each other (Boddy, 2000) resulting in reduced or increased secretion of lignin modifying enzymes depending on the type of interaction (Baldrian, 2004; Fukasawa et al., 2009; Hiscox et al., 2015). This may explain the disconnection between fungal community structure and lignin modifying enzyme activities.

Our results identified important wood physico-chemical properties correlating the fungal communities in all studied regions. These include extractives, total lignin, pH as well as decay class and its correlating factors remaining mass and density (the decay class increases with decreasing remaining mass and density). These correlations are consistent with previous studies conducted in Finland that investigated wood-inhabiting fungal communities in Norway spruce logs (Rajala et al., 2011, 2012). N and Zn were identified as important macro- and micronutrient for wood-inhabiting fungal communities in our data set. Nitrogen is a very limited macronutrient in early decay of beech wood and can be accumulated over time (Lombardi et al., 2012). It is important for fungi and other microbes as it is incorporated in many polymers including carbohydrates (e.g. chitin), proteins, lipids (e.g. sphingolipids), and nucleic acids (Prescott et al., 1999; Purahong et al., 2015b). Zinc on the other hand is an important structural component of fungal proteins, which are called zinc-binding proteins (Staats et al., 2013), e.g. zinc finger transcription factors. These transcription factors play important roles in many biological processes in fungi, such as sugar and amino acid metabolism, nitrogen utilization and cell division (MacPherson et al., 2006). Furthermore, Zn is present in peptidases and dehydrogenases (Hartikainen et al., 2012). Other macro- and micronutrients correlated significantly with the fungal community structure only in one region. This perhaps indicates the importance of other environmental factors such as soil characteristics, nutrient content, the amount of organic matter that can be heterogeneously distributed in different regions and under different climatic conditions (Fischer et al., 2010). The macro- and micronutrients might be either sufficient in wood and/or certain wood-inhabiting fungal species may overcome nutrient limitation in deadwood by translocating nutrients from soil and other substrates (Cairney, 2005; Boberg et al., 2010).

In conclusion, our work demonstrates that the relations of wood-inhabiting fungal community structures and their lignin-modifying enzyme activities are complex ecological and biochemical processes, which are controlled by various factors. Although the wood-inhabiting fungal community structure appeared to be similar across distinct geographical regions, the observed correlations between structure and wood physico-chemical properties were not identical across all regions. However, our analysis identified strong correlations of some factors (e.g. decay class, density, extractives, total lignin, pH) that were consistent across all regions. On the other hand, relations/parameters explaining enzyme secretion patterns, and thus actively mediated ecosystem processes varied strongly between the analysed regions. Nevertheless their action finally results in the decomposition of the wood. We also found that the wood-inhabiting fungal community structures did not sufficiently explain lignin-modifying enzyme activities, thus we hypothesized that the interspecific interactions and the priority effects may play more prominent roles (Hoppe et al., 2015b). Sequence based studies will be needed to disentangle the effects of interspecific interactions in wood-inhabiting fungal communities on enzyme activities and wood decomposition rates.

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Supplementary data

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